43. Contributions to the Visceral Anatomy and Myology of the Marsupialia. By CHARLES F. SONNTAG, M.D., F.Z.S., Anatomist to the Society.

[Received October 5, 1921: Read November 22, 1921.]

(Text-figures 70–79.)

CONTENTS.

	Page	1	Page
Ventral Mesentery	851	Urinary Organs	
Adipose Tissue	851	Ductless Glands	868
Cervical Lymphatic Glands	851	Respiratory Organs	870
Muscular System	852	Vagus and Sympathetic	873
Mouth	854	Systematic	877
Salivary Glands	857	Summary and Conclusions	880
Alimentary Canal	861	Bibliography	881
Organs of Circulation	865		

The present paper is based on the examination of several Polyprotodont and Diprotodont Marsupials * which died in the Society's Gardens; and the material comprised both fresh and preserved specimens.

I have used my paper on the Koala and Vulpine Phalanger for purposes of comparison (15), and I have drawn attention to the differences between the anatomy of *Perameles obesula* and that of *Canolestes obscurus*, recently described by Osgood (9).

When the abdomen of *Dendrolagus ursinus* was opened an avascular peritoneal fold, representing the remains of the ventral mesentery, was seen running from the pelvic floor posteriorly to beyond the urinary bladder anteriorly. Beddard (1) observed a similar condition in *D. bennetti* and *Ornithorhynchus*.

Adipose Tissue:—Owen (10) states that the omentum of the Opossums has no fat when there are accumulations elsewhere. In *Petaurus sciureus* the omentum is heavily laden with fat, and there are deposits in other parts. The fat in the anterior part of the thorax contains the thoracic lobes of the thymus gland.

Cervical Lymphatic Glands:—The relative positions of the two groups of glands in the Marsupialia have already been described in my paper on the Koala (15), but the number of glands in each varies. The anterior group has only one in *Perameles obesula* and *Canolestes obscurus*, but several are present in *Dendrolagus*

* Didelphyidæ: Didelphys azaræ, D. marsupialis, D. albiventris, Metachirus opossum, Philander laniger, Marmosa elegans; Dasyuridæ: Dasyurus viverrinus, Sarcophilus harrisi; Peramelidæ: Perameles obesula; Macropodidæ: Macrops bennetti. M. giganteus, M. rufus, M. melanops, Dendrolagus ursinus, Onychogale lunata, Bettongia penicillata; Phalangeridæ: Petarus sciureus, P. brevieeps, P. brevieeps papuanus, Pseudochirus peregrinus, Phalanger orientalis, Petaurus anstralis. Duplicates of some adult forms, and a number of pouch specimens of different ages were examined.

ursinus. Phascolarctos cinereus has the greatest number in the posterior group, and the parathyroids may be included among them.

• The only Marsupial with exoccipital processes touching the deep aspect of the platysma is *Phascolarctos cinereus*.

The Muscular System.

As considerable attention has already been paid to the muscles of the Marsupialia, the present section is limited to some points in the myology of the head and neck.

The Platysma:-The origin, insertion, and relations are similar in all Marsupials, but the characters differ considerably. In Dendrolagus ursinus and Macropus rufus it is muscular in the face, but almost aponeurotic in the neck. In Perameles obesula, on the other hand, it is muscular and thick in the neck, but more aponeurotic and firmer in the face; and it arises posteriorly from an equally strong and thick panniculus carnosus. In some parts these muscles are nearly two millimetres thick, and it is difficult to tell where the one ends and the other begins. The panniculus is very thick over the pectoral region. These conditions are reversed in Canolestes obscurus, in which Osgood described a thin panniculus and platysma. The platysma of Surcophilus harrisi (text-fig. 70 A) is muscular throughout, and its fibres cross at the anterior extremity of the internamal space. Beneath it there lies a stratum of more or less transverse fibres which fuse with it at the sides of the neck. Although the latter cannot be traced to an attachment in the face, they may correspond to the sterno-facialis of some of the higher Mammalia, e.g. Octodon and the Carnivora. The condition present here may indicate that the sterno-facialis arises from the platysma by splitting.

The Sterno-mastoid and Cleido-mastoid :- Carlsson (2) showed that they are fused throughout the greater part of the neck in Dendrolagus dorianus and Petrogale penicillata, but not in Trichosurus vulpecula; and they are similarly fused in Dendrolagus ursinus. In a pouch specimen of Macropus giganteus they fuse much farther forwards; but the muscles of Petaurus sciureus run parallel to one another, and are only fused at their cranial insertions. Osgood (9) records a similar condition in Canolestes obscurus, so it differs greatly from that in Perameles obesula, in which the cleido-mastoid arises from the cephalo-humeral and fuses with the cranial end of the sterno-mastoid. In Philander laniger, Metachirus opossum, and Didelphys the sterno-mastoid, cleidomastoid, and cleido-occipital form a group of three almost parallel muscles traversing the neck obliquely from behind forwards. In all species examined except D. azaræ they had separate origins from the clavicle; but in that species the cleido-occipital was implanted by tendon into the cleido-mastoid at its posterior extremity.

The posterior triangle of the neck is obliterated in *Dendrolagus* ursinus and *Petrogale xanthopus*, in which the trapezius is in

contact with the sterno-mastoid. In all other Marsupials the posterior triangle is evident, and its most prominent structure is the external jugular vein. The descending cutaneous nerves emerge from between the muscles in *Dendrolagus* (text-fig. 74).

The Omo-hyoid is present in all Marsupials, and is strap-like or fusiform. A central tendon is present in Macropus rufus (19) and a slight one exists in Petrogale xanthopus (13). In a pouch specimen of Macropus giganteus (text-fig. 71a) it crosses the lateral thyroid lobe which projects beyond the pretracheal muscles, and Osgood (9) figures it crossing the anterior lymphatic gland in Canolestes obscurus.

The Sterno-hyoids form a uniform strip from origin to insertion in all Marsupials except a male pouch specimen of Macropus giganteus (text-fig. 71c), in which they diverge at their hyoid attachments, and the larynx protrudes between them. They are easily separated, as a rule, from the subjacent sterno-thyroids, but that cannot be done in Perameles obesula. This would show that these muscles arise from a single sheet by splitting.

In my paper on the Koala and Vulpine Phalanger (15) I showed that the mylo-hyoid, digastric, and sterno-hyoid muscles of the former form a thin sheet playing over, but in no way connected to the hyoid bone; but I did not observe this condition in any other Marsupial; it may also be an abnormality in the animal examined by me. And in no other were there so many small muscle bundles running between the digastric and surrounding muscles. The fusion of the digastric and mylo-hyoid supports Gegenbaur's view that these muscles were differentiated by splitting.

The Digastric has a small central tendon in Macropus, but none is present in Dendrolagus, Perameles, and Metachirus. In Petrogale xanthopus (13) there are small fibrous areas, but no true central tendon. The mandibular insertion is usually about half the length of the bone between the angle and the symphysis, and is usually muscular, but Osgood (9) gives a more extensive attachment from angle to symphysis in Canolestes obscurus; and the anterior part is more aponeurotic.

The Hyoglossus was absent in my specimen of *Phascolarctos* cinereus, and is not described in Macalister's paper on the same animal. It is present in all other Marsupials. Its absence in the Koala is probably due to the long interval between the tongue and the hyoid bone, which has few attached muscles.

Carlsson (2) described the myology of *Dendrolagus dorianus* in detail, and grouped the muscles in three sets :---

1. Those resembling the muscles of the terrestrial Macropodidæ and differing from those of the Phalangeridæ.

2. Muscles resembling those of the Phalangeridæ and differing from those of the terrestrial Macropodidæ.

3. Conditions which differ from those of the terrestrial Macropodidæ and Phalangeridæ, and are secondary adaptations for an arboreal life. My own observations on *Dendrolagus ursinus* confirm those of Carlsson.

The stylo-hyoid ligaments are most prominent in Phascolarctos cinereus.

I was unable to detect any condition foreshadowing the sternomaxillares of the Edentata in the insectivorous Peramehidæ.

The Mouth.

The lips are fleshy in all Marsupials, and the upper one is cleft to a variable depth in the Macropodida, but entire in all Polyprotodonts. An incipient cleft is present in *Canolestes obscurus*. They are relatively thicker and always entire in the new-born animal. They bear numerous hard, rounded, or pointed tubercles in many species; in the Didelphyida they are absent in *Metachirus opossum*, *Philander laniger*, *Marmosa elegans*, and *Didelphys marsupialis*, but they are situated close to the angles of the mouth in *Didelphys azare*. In *Dasyurus viverrinus* they are situated at the level of the canine teeth. They are close to the angles of the mouth in *Dendrolagus*, *Pseudochirus*, and *Trichosurus*. The largest tubercles observed by me were in *Dendrolagus ursinus*. They are never so numerous as the papille in the Felidæ. In some forms the lips have callous pads.

Both labial fremums are present in all genera except *Dendrolagus* and *Pseudochirus*, which have only the upper one. In the young animal it passes between the incisor teeth to be attached to the anterior end of the incisive palatal pad, but it is fixed to the gum in the adult. In a young *Epyprymums rufescens* it is continuous with the median crest, running back on the anterior end of the palate. The lower lip is united to the sides of the gums by comb-like crests in *Dendrolagus* and *Pseudochirus*, and these form shaggy pads in the vestibule (text-fig. 70 E, a).

Labial labrets are present in *Phascolomys* and *Canolestes*. Owen (10) pointed out that the labial glands are well developed in *Dasyurus*, but I did not observe orifices in *D. viverrinus*.

The mucosa lining the vestibule is smooth in all Didelphyide, Sarcophilus harrisi, Trichosurus vulpecula. and Petaurus sciureus. It is covered with innumerable closely-set, rounded papillæ of moderate size in Dasyurus viverrinus and Phascolarctos cinereus, but these are not arranged in rows like the papillæ of the Ungulata. In many Marsupials it is traversed by ridges of various kinds, which, in some cases, if not in all, are modified and fused papillæ. They are thick and entire in Perameles obesula and Petaurus breviceps papuanus, and the spaces between them probably serve as traps for insects in the former. Their free borders are nodulated in the latter. They are thin and comblike in Macropus, Epyprymus Pseudochirus, and Dendrolagus (text-fig. 70 D, b & E, b); and their function may be to keep the spaces between the teeth clear of food particles, for they fit into them.

Cheek-pouches have been described in several species. They are large in Chironectes (10) and Canolestes (9), intermediate in size in Phascolarctos, and small in Peragale lagotis (10); but I do not think that the small fossæ of Perameles obesula can be dignified by the name of cheek-pouches. Forbes mentions rudimentary ones in Phascolomys. No Marsupial has comb-like structures on the tongue like the Ungulata.

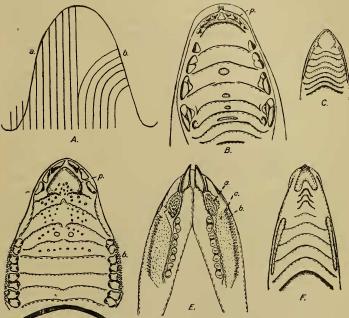
В. E., D.

A. The platysma of Sarcophilus harrisi showing superficial (a) and deep (b) fibre B-F. The palates of Sarcophilus harrisi (B), Onychogale lunata (C), Dendrolagus ursinus (D), and Macropus bennetti (F). E. Vestibule of Dendrolagus ursinus ; c. papillæ. Other letters in text.

The Hard Palate :- In many Marsupials the anterior end has an eminence, or "incisive pad," whose long axis usually coincides with that of the palate; it is at right angles to it, however, in Sarcophilus harrisi (text-fig. 70 B, p). It is smooth, papillose, or tuberculated, and varies greatly in prominence. In Phascolarctos cinereus and some of the Phalangeridæ it is replaced by a cluster of incisive tubercles, and its place is taken by a short, incisive ridge in *Epyprymnus rufescens*.

The complete palatal ridges are most numerous in the Perame-PROC. ZOOL. Soc.-1921, No. LVII. 57

Text-figure 70.



lidæ and *Caenolestes obscurus*, fewest in *Trichosurus vulpecula*, and largest in *Phascolarctos cinereus*, but the commonest number is eight. They are most variable in the Polyprotodonts, and the numbers of complete and incomplete ridges are of considerable value for purposes of classification, as shown in the table of formulæ given below.

In all Marsupials the ridges on the anterior part of the hard palate are larger than those on the posterior part, and the posterior margin of the palate frequently appears as a well-marked ridge. The spaces between the ridges are occupied by papillæ, tubercles, or incomplete ridges, and the latter are present in *Didelphys, Perameles, Dasyurus, Sarcophilus*, and *Canolestes*. The incomplete ridges cross the mid line, and differ from those of many of the higher Mammalia, in which they run from a median raphé to the sides of the palate.

No Marsupial has a median raphé running the whole length of the palate.

In a very young pouch specimen of Onychogale lunata the lips are entire, the tongue is excavated to form a bed for the nipple, and the incisive pad and anterior palatal ridges are outlined and hardly elevated; but the posterior palatal ridges are well-marked. The conditions are such that there is a firm area of contact between the nipple and mouth. In an older pouch specimen of *Macropus bennetti* the upper lip is cleft, the incisive pad is more prominent, and the anterior palatal ridges are more developed than those of *Onychogale*; and in pouch specimens of *Macropus giganteus* and *Phalanger orientalis* of still more advanced ages the conditions resemble those of the adult—namely, large incisive pads, strong anterior ridges, and weak posterior ones.

In animals requiring a firm contact between the mouth and nipples large anterior ridges would be disadvantageous, and they are unnecessary while the diet consists entirely of milk.

The vestibule and cavum oris communicate posteriorly behind the last molar teeth, and in several Marsupials the diaștemata form anterior communications.

The Soft Palate is frequently covered with papille, which are small, but visible to the naked eye. It has no uvula, and thins out posteriorly where it forms the anterior and lateral boundaries of the posterior extremity of the nasal tube; the orifice of the tube is round and small, or long and pyriform or slit-like. The larynx may be gripped by the tube, or the opening of the tube may overlap its superior aperture. In the mammary focus the larynx passes into the nasal tube so that the entrance of air is not impeded in suckling *.

In all Marsupials the orifices of the Eustachian tubes are within the nose. And these have been figured in my paper on

^{*} In a manuscript note Garrod states that the soft palate shuts off the glottis from the mouth in *Tamandua tetradactyla*, and suggests that this arrangement comes into use when the animal is collecting masses of termites before swallowing. No insects can possibly enter the larynx in consequence.

the Koala and Vulpine Phalanger (15). They are not surrounded by a cushion.

The characters of the palate can be conveniently expressed by means of formulæ. In the following list C denotes complete ridges, I incomplete ridges, P incisive pad, T incisive tubercles, R a median incisive ridge or raphé, and U uvula. For the area surrounded by the incisor and canine teeth the term "*incisire area*" is suggested.

POLYPROTODONTS.

DIPROTODONTS.

Metachirus opossum C_8I_0P U –	Pho
Philander laniger $C_s I_1 P + U -$	Tri
Didelphys azaræ $C_9I_1P + U -$	Pse
,, marsupialis $C_9I_1P + U -$	g
Marmosa elegans C_9I_0P-U-	Pet
Perameles obesula $C_{11}I_5P + U -$	
Dasyurus viverrinus $C_s I_3 P + U -$	p
Sarcophilus harrisi $C_7 I_5 P + U -$	Cœr
	$\mathcal{E}p$
	Den

Phascolarctos cinereus	C ₉ I ₀ TU-
Trichosurus vulpecula	
Pseudochirus pere-	
grinus ($C_8 I_0 P - U -$
Petaurus sciureus ($C_s I_0 TU -$
" breviceps pa-	
	$C_{s}I_{o}P + U - $
Cœnolestes obscurus ($C_{9}I_{5}P + U - $
Æpyprymnus rufescens ($C_7 I_0 RU -$
Dendrolagus (all	
	$C_{8}I_{0}P + U -$
Macropus (all species) ($C_s I_0 P + U -$
Onychogale lunata ($C_s I_o P + U -$
Phalanger orientalis (C_9I_0P+U-

The only Marsupial in the above list in which the palate narrows from before backwards is $\mathcal{E}pyprymnus rufescens$. In the Peramelids the palate is long and narrow.

I have nothing to add to existing descriptions of the tonsils and fauces. And in no Marsupial could I detect Waldeyer's lymphatic ring in the pharynx.

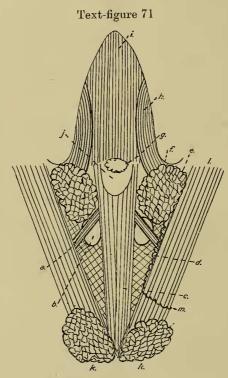
The Salivary Glands (text-figs. 71–74).

The Parotid Glands (m) are small in all Polyprodonts, but vary considerably in thickness and superficial extent in the Diprotodonts. They are thick, and extend from the auricles to the clavicles in *Dendrolagus* and *Dorcopsis*, and Garrod has figured their surface markings in the latter (4). Their relations in the former are shown in text-fig. 74; and the ducts, which are capacious and thin-walled within the glands, become thicker and contracted where they cross the masseter muscles. They are equally thick, but only reach the middle of the neck in *Phascolarctos cinereus*. And in none of these genera do they pass mesially to the inner borders of the sterno-mastoid muscles. In other genera they are thin, and cover a variable extent of the neck. They reach the clavicles in *Petaurus*, but do not extend so far in *Macropus*, *Epyprymnus*, and *Onychogale*.

The most extensive parotids are present in *Pseudochirus pere*grinus, in which they extend from the auricles to the clavicles,

57*

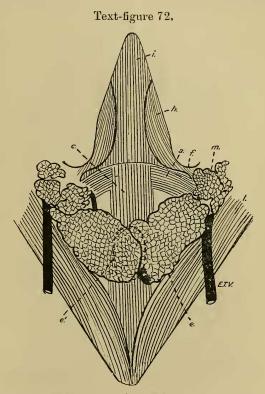
and pass inwards to cover the posterior fourth of the ventral surface of the neck. The glands are composed of numerous small portions surrounded by connective tissue, but it is not always possible to discern the ductules. They were prevented from reaching the mid line of the neck by the cervical thymic lobes in my specimen of *Trichosurus vulpecula*, but Symington (17) saw them cover the thymus in his. Although their extent is great they are thin.



The neck of Macropus giganteus. a. omo-hyoid; b. thyroid gland; c. pretracheal muscles; d. fascia; e. submaxillary gland; f. mandible; g. small gland; h. digastric; i. mylo-hyoid; j. larynx; k. cervical thymus; l. sterno-mastoid; m. parotid gland in outline.

The Submaxillary Glands (e) are, generally speaking, large in Polyprotodonts and small in Diprotodonts, but there are exceptions in the latter. They are large, single, and oval in the Didelphyidæ and Dasyuridæ, and in some of the former they reach from the angles of the mandible to the clavicles. They are immense and lobulated in *Perameles obesula* (text-fig. 72), in which a copious viscid secretion is required to surround and entangle the insects trapped in the cheek-pouches (?) and spaces between the palatal ridges and oral vestibule; and large glands are also present in the insectivorous *Canolestes obscurus* (9)*. In *Sarcophilus harrisi* the total mass of salivary glands is small, but the submaxillaries form the chief part.

In the Diprotodonts the submaxillary glands are single or lobulated, and the largest ones are present in the various species of



The neck of *Perameles obesula*. e'. concealed lobe of submaxillary gland; E.T.V. external jugular vein. Other letters as in text-fig. 71.

Dendrolagus. Small isolated glands are present between the main masses in *Macropus giganteus* (text-fig. 71, g), but the small glands are united to the main masses in *Dendrolagus ursinus* (text-fig. 74, g). And in these genera I traced small sympathetic

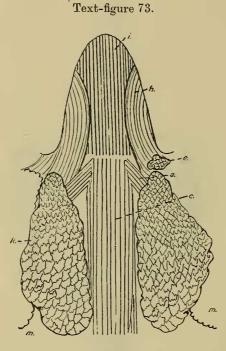
* In insectivorous Marsupials the glands are relatively smaller than those in the insectivorous Edentata.

nerves into the small glands (text-fig. 78, sgn). The ducts do not open on frenal lamellæ as in the Primates.

One must be careful not to confuse the submaxillary glands with the cervical lobes of the thymus gland, and histological examination must be carried out in doubtful cases.

The Sublingual Glands of many Marsupials have already been described, and Oppel (8) has collected the various observations.

In *Dendrolagus ursinus* they are long, thin, and narrow, and resemble those of D. *dorianus* already described by Carlsson (2).

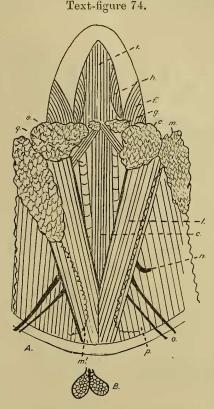


The neck of Petaurus sciureus. Letters as in text-fig. 71.

Osgood (9) described large round glands in *Canolestes obscurus*. Those of *Perameles obesula* are oval and do not extend so far forwards. Posteriorly they are in contact with the submaxillaries. The submaxillaries are large and the sublinguals small in *P. obesula*, but the conditions are reversed relatively in *C. obscurus*.

When the total bulk of the salivary glands of each Marsupial are compared, it is seen that *Dendrolagus* has the largest mass. And they conceal large areas of the muscles in the vicinity of the hyoid bone.

I have nothing new to add to our knowledge of the arterial supply and venous drainage of the salivary glands. And I could not detect any connection between them and the anterior cervical lymphatic glands.



The neck of *Dendrolagus ursinus* (A) and the cervical thymus B. *n*, *o*, cutaneous branches of the cervical plexus; *p*. trapezins; *q*. common carotid artery. Other letters as in text-fig. 71.

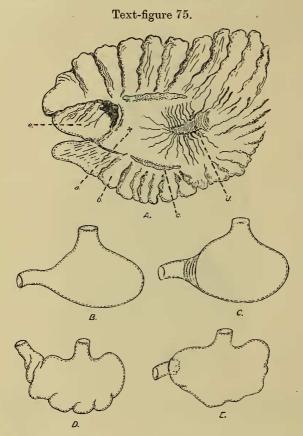
The Alimentary Canal.

The *Œsophagus*:—The mucosa of the abdominal part exhibits transverse rugæ in *Didelphys*, but in no other genus.

The Stomach:—The form depends on the degree of distension, but the latter is not stated in all existing accounts. Owen described a globular stomach in several species, but I found that the empty stomach is more or less triangular in a number of Polyprotodonts.

In Perameles obesula (text-fig. 75 B) the empty stomach is tri-

angular with the apex formed by the esophageal orifice. The left rounded basal angle represents the fundus, and the duodenum joins it at the right one. The pylorus does not project into the duodenum, and the sphincter is weak. The fundus is rugose. No gastric gland is present as in *Canolestes* (9), but there is a small lymphatic gland on the lesser curvature.



The stomach in the Marsupialia. A. Dendrolagus ursinus open to show—a, central tract; b. sacculi; c. gland strips; d. œsophagus; e. pyloric region. B. Perameles obesula. C. Metachirus opossum. D. Petaurus breviceps. E. Petaurus sciureus.

The empty stomach of *Metachirus opossum* (text-fig. 75 C) differs from the above in the thickness of the pyloric region, the existence of well-marked rugæ on both walls, and the great strength of the pyloric sphincter. There is a small lymphatic gland on the lesser curvature as in *Perameles obesula*.

In *Petaurus sciureus* (text-fig. 75 E) the globular fundus is directed forwards and to the left. The duodenum, whose commencement is notched, leaves its dorsal aspect. In *P. breviceps* (text-fig. 75 D) the duodenum has no notches, but a groove marks the pyloro-duodenal junction. The greater curvature is sacculated.

In Dendrolagus ursinus (text-fig. 75 A)* the greater part is concealed by the liver, the only parts visible being the cardiac cul-de-sac and greater curvature. The form and general characters resemble those of other species already described by Beddard (1), Owen (12), and Carlsson (2). These authors compared the stomachs with those of other Macropodidæ, and described the extent of the glandular and non-glandular parts of the mucosa.

Owen and Beddard described groups of follicular glands lying along the sides of the central tract (a) in *D. inustus* and *D. bennetti*. In *D. ursinus* they are replaced by long glandular strips (c), into which branches of the abdominal parts of the vagus nerves can be traced, and the vagus branches probably contain sympathetic fibres. From the examination of the stomachs of animals belonging to most of the mammalian orders, I have come to the conclusion that the branches of the vagi are greatly increased in numbers when there is a special gastric glandular apparatus. These branches pass directly to the glands as in *D. ursinus*, or run through a plexus with ganglia as in *Phascolarctos cinereus* (15). The pylorus does not project into the duodenum in *Dendrolagus*.

Osgood described a special gastric gland in *Coenolestes obscurus*, but did not mention its nerve supply.

The histology of the stomachs of the Marsupialia has already received considerable attention, and Oppel (8) has collected and analysed the various papers. I have nothing new to add to these accounts. Nematode worms are present in many stomachs.

The Intestinal Tract:—The observations recorded here are supplementary to those of Chalmers Mitchell (6, 7), Cunningham (3), Owen (10), and Flower (20).

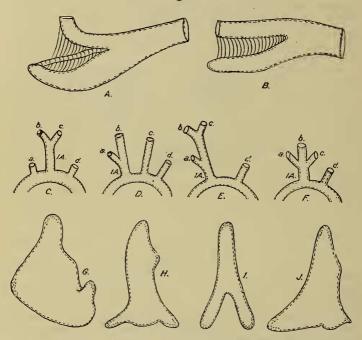
In Metachirus opossum the well-marked duodenal loop is wide, thin-walled, and extends posteriorly for a considerable distance. The flexure between its second and third parts is connected by the usual peritoneal ligament to the abdominal parietes and meso-colon, but is not continuous with the splenic ligament. The cæcum is two and a half inches long. It is capacious, and its interior is devoid of folds and septa. Meckel's Tract and the large intestine differ in no respect from that of *Didelphys* virginiana (6). The cæcum and Meckel's Tract is bisected by an artery (text-fig. 76 A).

The cæcum of *Perameles obesula* (text-fig. 76 B) is one and

* The specimen was specially hardened by injections of formalin to show the topography of the stomach.

three-quarter inches long. It is longer and thinner than that of *Peragale lagotis* figured by Chalmers Mitchell (6), and it has a mesentery whereas that of *P. lagotis* has not. In other respects the intestinal tracts of these Peramelidæ are similar. Their cæca differ from the minute conical appendage of *Cænolestes obscurus* as figured by Osgood (9), and the latter is devoid of a mesentery.

Text-figure 76.



A. Cæcum of Metachirus opossum; B. cæcum of Perameles obesula; C-F. aortic arches with innominate (IA), right subclavian (a), right common carotid (b), left common carotid (c) and left subclavian (d) arteries; G-J. the spleens of the Marsupials (names in text).

The ligament running backwards from the duodenum in *Perameles obesula* crosses the front of the rectum and fuses with the splenic ligament. They enclose a pocket containing the rectum, and a probe passed into it runs backwards into the pelvis.

The intestinal tract of my nearly adult female *Dendrolagus ursinus* differs in several respects from that of a young specimen described by Chalmers Mitchell (7). The duodenal loop is sharply differentiated, but runs insensibly into Meckel's Tract. The coils of Meckel's Tract do not form a double spiral, and there is only one cæcum. The latter is fusiform, but is devoid of longitudinal bands, sacculi, and a vermiform appendage, and the superior mesenteric artery does not occupy the free edge of its mesentery. At the point where the ileum enters the colon there is a transverse vein. At a point two inches proximal to the ileo-cæcal junction there is a single Peyer's Patch measuring one and a quarter inches in length.

No trace of a second cæcum was found in my pouch specimens of *Macropus bennetti*, *Macropus giganteus*, *Onychogale lunata*, and *Bettongia penicillata*.

I have refrained from giving a detailed list of the measurements of the different parts of the intestinal tract in my specimens as they had been preserved for varying periods. The data, if given, would be of little value in consequence.

The Pancreas.

In all Marsupials examined except *Phascolarctos cinereus*, I found the pancreas much subdivided and dendritic, but the arrangements of the subdivisions varied considerably. In *Metachirus opossum* they are aggregated to form a compact mass in the posterior part of the duodenal loop, and a long, narrow part stretches across the abdomen to the spleen. Small branches are given off from the body. The duct opens into the duodenum along with the common bile-duct. *Perameles obesula* also possesses a long, narrow body with lateral processes, and the duodenal • loop contains an almost complete ring of pancreatic tissue such as is found in some Rodents and Carnivora.

In Petaurus sciureus, P. breviceps, and P. breviceps papuanus the pancreas consists of long strips and small isolated pieces arranged along the course of the mesenteric vessels. It is difficult to detect the ducts of the small lobules, and it is impossible to do so when there is much fat in the omentum and mesentery. The same dendritic arrangement is seen in *Dendrolagus ursinus*, in which the pancreatic and common bile-ducts open separately into the duodenum. In *Macropus*, on the other hand, the ducts are confluent (Owen).

Osgood describes a dendritic pancreas in *Cænolestes obscurus* (9), so its condition is no more highly evolved than that of *Perameles obssula*.

It is evident, therefore, that the pancreas of *Phascolarctos* cinereus is of a higher type than the dendritic, more or less diffuse, organ of other forms.

The Organs of Circulation.

The *Pericardium* adheres to the diaphragm in all Marsupials except *Trichosurus vulpecula*, and it adheres to a variable extent to the sternum and ribs. In *Dendrolagus ursinus* and pouch specimens of *Macropus giganteus* and *M. bennetti* the lungs were seen to overlap the base of the heart, and the precordia, or uncovered part, was adherent to the sternum and ribs. The Heart:—In all Marsupials the apex is formed by the left ventricle, and the right ventricle falls short of it by a variable interval. Cunningham (3) states that the right ventricle in *Thylacinus* stops short of the apex by $1\frac{1}{2}$ inches, but I never observed such a long interval in any Marsupial. In very young pouch specimens the right ventricle is relatively longer than in adults.

Owen (11) describes bifurcation of the right auricular appendix as one of the chief characteristics of the Marsupial heart, but some species have no trace of a division, and in others the division has no reference to the ascending aorta.

The appendix is conical and bifid in *Petaurus sciureus* and pouch specimens of *Macropus bennetti* and *Macropus giganteus*, but the two divisions are small. In *Dendrolagus ursinus* and *Perameles obesula* it is large and round; and the former has a well-marked process lying on the dorsal aspect of the aorta, but no trace is present in the latter. Cunningham pointed out that there is no bifurcation in *Thylacinus* and *Dasyurus*, but there is a strong division in *Cuscus* and *Trichosurus*. A slight division is present in *Phascogale*, but it has no reference to the ascending aorta (3). In *Phascolarctos cinereus* the secondary process is large, and the right precaval vein passes into it.

The characters of the interior of the auricles and ventricles of many Polyprotodonts and Diprotodonts have already been described by Cunningham.

The Aortic Arch:—In all Marsupials it describes a full curve and ends at the level of the fourth dorsal vertebra, and the relations are similar in all forms to those described in the Koala (15). The branches differ considerably, for six types are present, as shown in text-fig. 76 C-F.

1. Both carotids and subclavians arise separately, so no innominate artery is present—*Phascolarctos cinereus* †.

2. The two subclavian and the innominate arteries are given off, and the latter divides into the two common carotid arteries— Dasyurus macrurus (C).

3. The branches arise as in Man--Phascolarctos cinereus*, Petaurus breviceps*, and Phascolomys mitchelli (D).

4. The innominate artery gives off the left common carotid artery, and divides into the right subclavian and right common carotid arteries— $Trichosurus vulpecula \dagger$.

5. The innominate artery gives off the right subclavian artery, and is continued as the bicarotid trunk which divides into the two common carotid arteries—*Thylacinus harrisi*, *Didelphys cancrivora*, *Dasyurus viverrinus*, and *Petaurus anstralis* * (E).

6. The innominate artery gives off the right subclavian and both common carotid arteries at the same level—*Cuscus maculatus, Dendrolagus ursinus, Phascolarctos cinereus* *, and *Macropus giganteus* (F).

* These observations are recorded in hitherto unpublished notes by Garrod.

† These types have been figured in my paper on the Koala.

The left subclavian artery is the only constant branch, and the left superior intercostal artery sometimes arises from the arch a little distal to it.

I agree with Cunningham that there is no trace of the obliterated ductus arteriosus. And I have nothing to add to existing descriptions of the remainder of the arteries.

The Vena Transversa is usually horizontal and drains the mouth, tongue, salivary glands, and some of the cervical muscles. In a few cases it receives laryngeal veins. In some specimens of *Trichosurus vulpecula* it is connected to the internal jugular veins by vessels corresponding to the anterior jugular veins of the Ocelot and Man. I have already figured these in my paper on the Koala and Vulpine Phalanger (15).

The External Jugular Veins in all Marsupials are similar to those described in my paper on the Koala.

In all Marsupials examined by me there are two *precaval veins*, but Garrod mentions in a hitherto unpublished note that the two innominate veins unite about half an inch in front of the heart to form a single precaval vein in *Petaurus breviceps*.

The Postcaval Vein covers the posterior half of the abdominal aorta in all Marsupials examined by me except *Phascolarctos* cinereus, and Hochstetter found it covering the aorta in all except *Petaurus taguanoides*. Beddard found it covering the aorta in all his specimens.

The Urinary Organs.

The *kidneys* are conglobate in all Marsupials, and their relative positions vary as follows :---

1. Right kidney entirely anterior to the left one - Phascolarctos cinereus.

2. Posterior pole of right kidney level with the hilum of the left one—Metachirus opossum, Marmosa elegans, Perameles obesula, Petaurus sciureus, and Trichosurus vulpecula.

3. Both kidneys situated at the same level—Macropus giganteus, Macropus bennetti, Dendrolagus ursinus, and Cænolestes obscurus.

On section only one papilla is present, and it may be sharp and conical, or broad and flat. Small nodule-like elevations may be present on broad, flat papillæ. No fat is present in the kidney pelves in any of my specimens.

The course of the *ureters* is similar to that already described in my paper on the Koala and Vulpine Phalanger (15).

The ventral surface of the bladder is connected to the ventral abdominal wall by a ligament, which varies in prominence in different species. It is thin in the Polyprotodonts and thick in *Dendrolagus ursinus*. In that species, as in *D. bennetti* (1), its attachment to the abdominal wall is very extensive. In all species it is completely anangious. It represents the remains of the ventral mesentery. Lateral vesical ligaments are absent. The dorsal surface of the bladder of *Dendrolagus ursinus* is connected to the dorsal abdominal wall at the sides of the vertebral column by two strong ligaments, which divide the pelvic cavity into a median and two lateral compartments. The central one contains the rectum and uterus, and the oviducts curl over the free edges of the ligaments.

In *Perameles obesula* the uterus is separated from the rectum by the wall of the peritoneal pocket formed by the fusion of the splenic and duodenal ligaments.

I have nothing to add to the existing descriptions of the generative organs of either sex, nor to Osgood's *résumé* of our knowledge of the marsupial bones (9). In the latter paper the nipples are also enumerated, and it is shown that they are asymmetrically arranged in the Didelphyidæ alone.

• The Ductless Glands.

The suprarenal capsules are situated on the mesial aspects of the anterior poles of the kidneys in all Marsupials examined by me except *Phascolarctos cinereus*, and that species has a very prominent ligament uniting the left kidney and its capsule.

The Thymus Gland.

The Polyprotodonts differ from the Diprotodonts in the characters of the thymus gland. In the former it consists of two elongated or oval bodies in the anterior part of the thorax, but in the latter there are two cervical lobes in addition; and one must be careful to distinguish them from salivary glands. Osgood (9) found four thoracic glands in *Canolestes*.

Topography:—The cervical lobes lie immediately under cover of the platysma. They are oval or pyriform, with the narrow ends turned forwards. They lie at the root of the neck, as in *Dendrolagus ursinus* (text-fig. 74 B), *Macropus giganteus* (text-fig. 71, k), and *Macropus rufus*, or they may extend far forwards and even conceal one of the submaxillary glands, as in *Petaurus sciureus* (text-fig. 73, k). They may touch the parotid glands anteriorly, or be in contact with them throughout the entire length of the neck as in *Trichosurus vulpecula*. In *Pseudochirus peregrinus* they are concealed by the parotid glands. They may be in contact with the mid line, or an interval in which the pretracheal muscles are seen may separate them. The subjacent structures are the sterno-mastoids, pretracheal muscles, and part of the sternum and clavicles.

The surfaces may be finely or coarsely lobulated, and in no case were they invested by a connective-tissue capsule derived from the cervical fascia.

Symington (17) described and figured the topography of the thoracic lobes, and described the gland in a number of Marsupials. His observations on the Polyprotodonts are limited to *Didelphys* virginiana and *Dasyurus cancrivora*. He could not detect cervical

lobes in either of these species, and I was unable to detect them in the Didelphyidæ, Dasyuridæ, and Peramelidæ. He believes that the primitive condition is present in the Dasyuridæ, and the cervical lobes of the Diprotodonts are a specialization in association with the vegetable diet and the call for a larger amount of thymic tissue. If, as Swale Vincent suggests, the cervical and thoracic lobes perform different functions, it is difficult to ascribe any use other than dietetic to the former.

The Thyroid Gland.

In *Perameles obesula* the left lobe is long and narrow, but the right one is short and oval, and partly under cover of the pectoralis major. No isthmus is present; and this arrangement is the reverse of that which I have already described in *Phascolarctos cinereus* (15).

In all other Marsupials, I found the gland to be composed of two small, oval lobes lying on the sides of the larynx alone (*Petaurus sciureus*), or the posterior part of the larynx and a variable number of tracheal rings; and the only animal possessing an isthmus is *Trichosurus vulpecula*.

Each lobe receives a single artery from the common carotid, and the veins join the internal jugular veins.

The lobes were concealed by the pretracheal muscles in all animals examined except a male pouch specimen of *Macropus* giganteus.

The Spleen (text-fig. 76 G–J).

The observations recorded here are supplementary to those of Colin Mackenzie (5), Owen (11), and Retterer (21).

In most genera there is little variation in form in the various species, but the spleen has different shapes in the species of *Dendrolagus*. In *D. ursinus* it is long and **Y**-shaped, with rounded extremities (text-fig. 76 I). In *D. inustus* (12) it is **T**-shaped, and it is spoon-shaped in *D. bennetti* (1). Carlsson (2) states that it is pointed in *D. dorianus*.

In *Petaurus sciureus* (text-fig. 76 J), *P. breviceps*, and *P. breviceps* papuanus the spleen is triangular, with sharp angles not prolonged into processes, and the base of the triangle is applied to the greater curvature of the stomach.

The spleen of *Phalanger orientalis* resembles those of the Petaurists, the only difference being that its apical angle is 90°, whereas those of the latter are larger.

Colin Mackenzie described and figured the spleen of *Macropus* and my specimens differ in no way from his description; and a pouch specimen of *Onychogale lunata* has a **Y**-shaped spleen similar to that of the Kangaroos. The form does not alter from birth to adult life. In *Perameles obesula* (text-fig. 76 G) the spleen has a massive triangular body with thick sides, and the angles are prolonged by cylindrical or flattened processes of splenic tissue. If the processes are removed, the resulting organ resembles that of *Phascolomys* described and figured by Colin Mackenzie. Garrod states in a hitherto unpublished note that the spleen of the Wombat forms an equilateral triangle. In a specimen of *Phascolomys mitchelli* it had a lateral piece. In *Perameles nasuta* it is thin and triangular, without prolongations.

The Bandicoots are the only Marsupials in which I observed a continuity between the splenic and duodenal peritoneal ligaments. And the looseness of connection between the spleen and stomach differs considerably; these viscera were very closely united to one another in *Dendrolagus ursinus*.

Osgood (9) showed that the spleen of $Canolestes \ obscurus$ has an elongated body and a lateral piece, so it differs from that of *Perameles obesula*.

In *Metachirus opossum* it is \mathbf{T} -shaped, with one of the horizontal limbs short (text-fig. 76 H).

The external appearances of the spleens differ considerably even in different species. Histological examination of the spleens of many Marsupials shows that there is a very strong trabecular network.

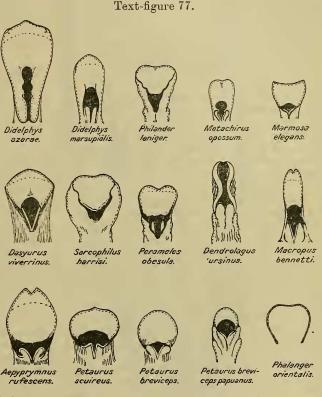
The Respiratory Organs.

The *epiglottis* is large, and its apex, which is entire or notched, is frequently emarginate. It lies vertically or inclined forwards, and it is sometimes gripped by the posterior extremity of the nasal tube. And it is closely related to the base of the tongue in all Marsupials except *Phascolarctos cinereus*. As the form of the epiglottis and prominence of the aryteno-epiglottic folds vary, the shape and size of the superior aperture of the larynx differ considerably (text-fig. 77).

In Didelphys azaræ the epiglottis is large, conical, connected to the arytenoids by prominent ligaments, and strongly emarginate, without any trace of a notch. The superior aperture of the larynx is long and narrow, and cuts into the posterior surface of the epiglottis. In *D. marsupialis*, on the other hand, the entire epiglottis is only slightly emarginate, the arytenoid cartilages are plainly visible, and the superior laryngeal aperture is wide and round. In *Philander laniger* and *Marmosa elegans* the epiglottis is broad, and its apical margin is slightly concave but not emarginate; and the superior aperture of the larynx is triangular. Their condition is intermediate between those of *Didelphys* and *Metachirus opossum*, in which the non-emarginate apex of the epiglottis is notched. The epiglottis, therefore, is of considerable value for differentiating the genera of the Didelphyidæ from one another.

The epiglottis is large, prominent, and entire in the Dasyuridæ. In *Dasyurus viverrinus* it is uniformly thick and the apex is

slightly emarginate. Its connections to the arytenoid cartilages are also thick, and the superior aperture of the larynx is large and open. The rima glottidis has very thick boundaries. In Sarcophilus harrisi, on the other hand, the epiglottis is large and thin, and its posterior parts are folded inwards and lean against the anterior parts, so the superior aperture of the larynx is a transverse slit. And the arytenoid cartilages and rima glottidis are entirely concealed.



The larynx of the Marsupialia. The convex dotted lines crossing the epiglottis are the levels of emargination.

The epiglottis of Perameles obesula has a broad, emarginated, notched apex; and there is a small fossa with a crescentic orifice between the epiglottis and the tongue. The characters of the fossa in *P. lagotis* have already been described by Owen (10).

In the Macropodidæ there is considerable variation in the characters of the epiglottis. In *Dendrolagus ursinus* it is entire and the sides are folded inwards, so the superior laryngea 58

PROC. ZOOL. Soc.-1921, No. LVIII.

aperture has the form of the figure 8, and the rima glottidis is invisible. In *Epyprymnus rufescens*, *Macropus bennetti*, and *Macropus giganteus* the apex of the prominent epiglottis has a small sharply-cut notch resembling that in *Trichosurus vulpecula*, and much emargination is present. The notches in the Polyprotodont, on the other hand, are wider and shallower.

Owen (10) states that the epiglottis of the Phalangers is broad and bifid, but I found it entire and slightly concave in a mammary factus of *Phalanger orientalis*. It is entire in *Pseudochirus* peregrinus, *Petaurus sciurens*, *Petaurus breviceps*, and *Petaurus* breviceps var. papuanus. In *Petaurus sciureus* the degree of emargination is considerable.

The large entire epiglottides in *Phasolarctos cinereus* (15) and *Coenolestes obscurus* (9) have already been described.

The characters of the other cartilages, and the cords, ventricles, and muscles are described by Owen.

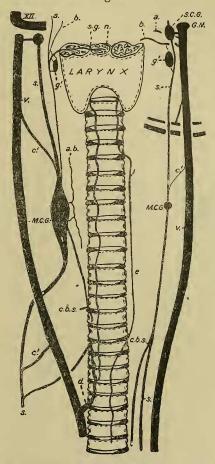
The trachea is usually long and narrow, but it is short and wide in *Phascolarctos cinereus*. The cartilages frequently form complete rings, but in many species they are defective behind and a membrane fills the gap. Some of the rings are expanded and thickened on one side, and the numbers observed were :— Metachirus opossum 19; Perameles obesula 34; Petaurus sciureus 35; Dendrolagus ursinus 35. The numbers in other Marsupials have been recorded by Cunningham (3), Osgood (9), and Owen (10). In Marsupials in which the vagus and sympathetic are separate, the tracheal and pulmonary plexuses are large.

The Lungs:—My observations differ from those of Owen (10) in a number of cases. In the Didelphyidæ the right lung is trilobate and has a well-marked azygos lobe. The left lung is entire in Metachirus opossum, but is bilobate in Marmosa elegans. In Perameles obesula the right lung has three lobes and an azygos appendage, and the left one is entire; Owen also states that the left lung of Perameles is undivided. The Phalangeridæ have bilobate left lungs, and the right ones are trilobate with the azygos lobe in addition. In the Macropodidæ, of which Dendrolagus ursinus, Macropus bennetti, and Macropus giganteus were examined, both lungs have deep median sulci dividing them into anterior and posterior parts, but these are not entirely separated from one another, and the azygos lobe is large. The conditions differ from those of other Kangaroos described by Owen (10). The mesial borders of the lungs are thin in the Macropodidæ.

The division of the lungs appears to differ considerably even in the same species. Osgood (9) observed variations in *Canolestes* obscurus, and Owen, Forbes, and I have recorded three different arrangements in *Phascolarctos cinereus*. I am unaware of any account of the lobes of the lungs of the uterine fetus, and it is important to ascertain whether there is fusion of lobes of the left lung during development similar to that which takes place in *Bradypus tridactylus*, in which the feetal lungs are divided into lobes; but those of the adult are entire.

In a *Dendrolagus ursinus* hardened by formalin injections it is seen how the lungs conceal the large vessels and part of the right auricular appendix.

Text-figure 78.



The cervical parts of the vagi and sympathetics in *Dendrolagus ursinus*. Letters in text.

The Vagus and Sympathetic Nerves*.

No account of the viscera of any animal is complete without a description of these nerves, which control their activities.

The cervical parts are arranged in two ways in the Marsupialia.

* The lettering on text-figs. 78 and 79 corresponds, so far as possible, to that of text-figs. 62 and 63 in my paper on the Koala (15).

In the first type, which is present in both Polyprotodonts and Diprotodonts, they are fused to form vago-sympathetic cords. In the second form, which is found only in Diprotodonts, they are connected by a variable number of communicating branches. In no Marsupial did I find both types present in the neck as I observed them in *Tamandua tetradactyla* and *Lutra maculicollis*. These forms were present as follows in my specimens:—

Type 1:—Metachirus opossum, Didelphys azaræ, Didelphys marsupialis, Philander laniger, Dasyurus viverrinus, Sarcophilus harrisi, Perameles obesula, Phascolarctos cinereus, Trichosurus vulpecula, and Petaurus sciureus.

Type 2:—Dendrolagus ursinus, Macropus giganteus, Macropus bennetti, Pseudochirus peregrinus, and Æpyprymnus rufescens.

The course of the vagi from the base of the skull to the point where they reach the cosphagus in the posterior part of the thorax has already been described in my paper on the Koala (15), but the branches vary considerably.

The vagus (V) and hypoglossal (XII) nerves are fused in *Phascolarctos cinereus*, but branches of communication run between them in other Marsupials.

In *Dendrolagus ursinus* the pharyngeal (a) and superior laryngeal (b) nerves are given off from the sympathetic on the right side, but from the vagus on the left. The cord giving off the right nerves supplies the submaxillary glands (s.g.n), and possesses a ganglion (g'); it probably contains vagus fibres.

The vague and sympathetic communicate. In the first type branches run between the vague and superior cervical ganglion (s.c.g). In the second type there are several branches of communication (c') throughout the neck as well.

At the root of the neck the right vagus gives off its recurrent branch (d), and the vago-sympathetic cord is resolved again into its component vagus (v) and sympathetic (s) elements. I observed no communications between the right and left recurrent laryngeal nerves, but the right nerve and sympathetic cord communicated.

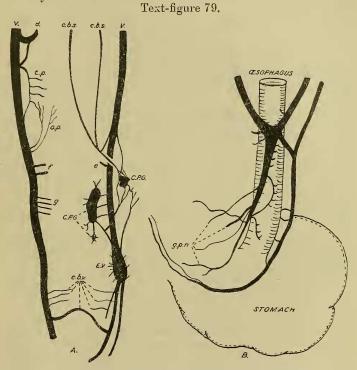
Cardiac Nerves:—In type 1 the vagus transmits sympathetic cardiac nerves, but in type 2 (text-fig. 79) the cardiac branches of the vagus (f) and sympathetic are separate throughout. And the cardiac branches of the sympathetic (c.b.s) come from the middle ganglion or main cord, but never from the superior ganglion. The cardiac and pulmonary plexuses have well-marked ganglia in *Dendrolagus ursinus*, and that species has large tracheal and cesophageal plexuses.

The Posterior Thoracic Parts of the Vagi:—In the Koala, as in some reptiles, birds, and Man (Wirsung's case), they are fused to form a combined trunk; but the trunk of the Koala is not resolved again into the two vagi. And many gastric nerves are given off in the thorax.

In *Metachirus opossum* the left vagus runs along the ventral surface of the esophagus. It gives off a branch which accom-

panies the right vagues on the dorsal aspect on the coophagues. And no branches of communication run between the vagi^{*}. In *Perameles obesula* the cords have a similar disposition, but communicating branches run between them.

The conditions are more complex in *Dendrolagus ursinus* (text-fig. 79 A). The vagi are linked together by numerous branches of communication (c.b.v). The left one has a large oval expansion (EV) beyond which it bifurcates, and the right half fuses with the right vagus. The branches of supply to the coophagus are very numerous.



The vague and sympathetic in *Dendrolaque ursinus*. A. In anterior two-thirds of thorax. B. Posterior thoracic and abdominal parts. *op.* œsophageal plexus; *tp.* tracheal plexus; *f.* right cardiac branches of vagues; *g.* pulmonary nerves; C.P.G. ganglia of cardiac and pulmonary plexuses. Other letters in text.

In no case did I find any communication between the vagus and phrenic nerves.

Abdominal Parts of the Vagi:—The vagi terminate in three ways in the Marsupialia. The combined trunk ends in the solar plexus, and gives branches to the stomach in the Koala as in some

* In Nandinia binotata, the most primitive Carnivore, the conditions resemble those in Metachirus.

lower Vertebrata. In *Metachirus opossum* and *Perameles obesula* the left vague ends in the ventral wall of the stomach, and the right one gives branches to the stomach and ends in the solar plexus. In the third type, which is exemplified by *Dendrolagus wrsinus* (text-fig. 79 B), the main masses of the vagi end in the stomach, and branches of communication run to the solar plexus. Numerous branches (g.p.n) run to the special gastric gland.

I never observed any other mode of termination in the Mammalia, but the branches of communication between the vagi and the abdominal sympathetic plexus are more numerous in some of the Eutheria.

The Cervical Sympathetic:—The arrangement in animals with the first type is figured in my paper on the Koala (15), and that in the second type is shown in text-fig. 78.

The superior cervical ganglion (S.C.G) is always present; the inferior one is frequently present, but the middle one (M.C.G) is very variable. It is well-marked in *Dendrolagus ursinus*, but absent in *Æpyprymnus rufescens*. In a pouch specimen of *Macropus giganteus* it appears as a slight increase in the diameter of the nerve. When both middle ganglia are present one may be minute and give off no branches. The branches of the cervical sympathetic are :—

1. Communicating to the cervical plexuses, vagi, and right recurrent laryngeal nerve.

2. Branches accompanying the common carotid (a.b), subclavian, and vertebral arteries.

3. Cardiac nerves (c.b.s.) which arise from the middle or inferior ganglia or main cords themselves.

I was unable to trace the filaments accompanying the vertebral arteries to the brain. In some higher Mammals they can be traced nearly to the interpeduncular space.

The sympathetic cords terminate in one of three ways. They may end in the solar plexus and give off no branches to the aortic plexus; and in this and the next form no splanchnic nerves are present. In the second type the main mass of the sympathetic ends in the solar plexus, but sends a small communication branch to the aortic plexus. In the third type, which is the commonest, the cords run back to the sacral region, and splanchnic nerves are present.

It has been shown by Volkmann, Bidder, and others that the sympathetic becomes included more and more in the vagus as we descend the vertebrate scale, and I believe that the form in which they are fused in the neck is more primitive than that in which they are separate. The nerves are fused in the neck in Ornithorhynchus (Knox).

In *Dendrolagus ursinus* the phrenic nerves bifurcate beyond the roots of the lungs, and the halves pass to the ventral and dorsal parts of the diaphragm. The nerve to the omo-hyoid comes from the cervical plexus, and has no connection with the hypoglossal nerve as in *Petrogale xanthopus*.

Systematic.

When the structures described above are arranged in systematic order, the following results are obtained :---

Sub-order POLYPROTODONTIA.

Characters common to all Genera:—Lips entire. Both frenums present. Three circumvallate papillæ, a well-developed sublingua, and no lateral organs. Tonsils compact. Stomach simple and has no special gland. Parotids small. Submaxillaries large. Intestinal tract short. No cervical thymus. No thyroid isthmus. Post-caval vein covers aorta. Vagus and sympathetic fused.

Family DIDELPHYIDÆ.

Characters common to all Genera :--Oral vestibule smooth. No cheek-pouches. Duodenal loop differentiated. Cæcum welldeveloped. Thyroid gland anterior. Mammæ asymmetrical. Patella not ossified.

Genus *Didelphys*:—Labial tubercles variable. Palatal formula C_gI_P+U- . Epiglottis conical, entire, emarginate. Lower esophagus transverely rugose. Mammæ 5–13.

Genus Metachirus:—No labial tubercles. Palatal formula C_sI_0P-U- . Epiglottis notched. Lower œsophagus not transversely rugose. Mammæ 7–9.

Genus Philander:—No labial tubercles. Palatal formula C_sI_1P+U- . Epiglottis has concave anterior border and rounded angles. Lower æsophagus not transversely rugose. Mammæ 7.

Genus Marmosa:—No labial tubercles. Palatal formula $C_{g}I_{o}P-U-$. Epiglottis with concave anterior border and sharp angles. Lower æsophagus not transversely rugose. Mammæ 9–15.

Family DASYURIDÆ.

Characters common to all Genera:—No cheek-pouches. Duodenal loop not differentiated. Cæcum absent. Thyroid gland anterior. No transverse æsophageal rugæ. Mammæ symmetrical. Patella not ossified.

Genus *Dasyurus*:—Labial tubercles opposite canine teeth. Oral vestibule papillose. Palatal formula $C_s I_3 P + U - .$ Epiglottis thick, rounded, entire. Mamme 6-8.

Genus Sarcophilus:—No labial tubercles. Oral vestibule smooth. Palatal formula $C_{r}I_{s}P+U-$. Epiglottis thin and parts crushed together. Mamme 4.

Family PERAMELIDÆ.

Genus Perameles :---No labial tubercles. Oral vestibule with hard ridges. Cheek-pouches (?) small fossæ. Palatal formula $C_{11}I_sP+U-$. Epiglottis notched. No transverse æsophageal 878

rugæ. Duodenal loop differentiated. Cæcum well-developed. Spleen massive and triangular. Thyroid gland posterior. Mammæ symmetrical. Patella ossified. Mammæ 6-8.

Sub-order DIPROTODONTIA.

The Diprotodontia have few characters common to all their genera in contradistinction to the Polyprotodontia. And these characters are :—Parotid glands large. Tongue has reduction in the sublingua and shows lateral organs. Thymus gland has two cervical and two thoracic lobes. Meckel's Tract long. Cæcum large.

Family MACROPODIDÆ.

Characters common to all Genera:—Lips cleft. No cheekpouches. Oral vestibule ridged. Œsophagus has no transverse rugæ. Stomach sacculated. Lungs have small degree of division. Vagus and sympathetic nerves separate. Thyroid gland anterior and has no isthmus. Mammæ symmetrical. Patella not ossified.

Genus *Macropus*:—Both labial frenums present. Palatal formula C_sI_oP+U- . Epiglottis notched and wide. Spleen with lateral process. Stomach has patches of follicular glands and the area of digestive epithelium is small. (Esophagus enters stomach near cardiac end. Mammæ 4.

Genus Dendrolagus:—Large labial tubercles. No lower labial frenum. Palatal formula $C_{s}I_{o}P+U-$. Epiglottis entire and folded. Stomach with large area of digestive epithelium and follicular glands in patches or strips. Spleen Y-, T-, or spoon-shaped. Œsophagus enters stomach near cardiac end. Mamme 4.

Genus $\mathcal{E}pyprymnus :$ —No labial tubercles. Both labial frenums present Palatal formula $C_{\gamma}I_{0}RU$ —. Epiglottis wide and notched. Œsophagus enters stomach near pyloric end.

Family PHALANGERIDÆ.

Characters common to all Genera:—Lips entire. No cheekpouches. Œsophagus has no transverse rugæ. Stomach simple and has no special gland. Duodenum not a very specialized loop. Meckel's Tract short. Cæcum well-marked. Mammæ symmetrical. Patella not ossified.

Genus *Petaurus*:—No labial tubercles. Both labial frenums present. Oral vestibule smooth. Palatal formula varies. Epiglottis entire and rounded. Spleen an isosceles triangle. Vagus and sympathetic fused. Mammæ 4.

Genus Pseudochirus:—Lower labial frenum absent. Large labial tubercles. Oral vestibule ridged. Palatal formula C_sI_oP-U- . Epiglottis entire. Vagus and sympathetic separate. Mamme 4.

Genus *Phalanger*:—Both labial frenums present. No labial tubercles. Oral vestibule smooth. Palatal formula C_0I_0P+U- . Epiglottis with shallow notch. Spleen a rectangular scalene triangle. Vagus and sympathetic fused. Mamma 4.

Genus *Trichosurus*:—Both labial frenums present. Labial tubercles present. Oral vestibule smooth. Palatal formula $C_{s}I_{0}P-U-$. Epiglottis with sharp notch. Spleen with lateral piece. Vagus and sympathetic fused.

Family Phascolarctidæ.

Genus *Phascolarctos* :—Both labial frenums present. No labial tubercles. Oral vestibule papillose. Palatal formula C_0I_0TU- . Epiglottis large, entire, emarginate. Spleen an isosceles triangle. Stomach has a special gastric gland. Vagus and sympathetic fused. Mammæ 2 and are symmetrical. Patella absent.

Osgood (9) described the resemblances between *Conclestes* obscurus and modern Peramelids, and the following table shows the differences between it and *Perameles obesula*:---

Perameles obesula.

- 1. Four large follicles in the submental triangle.
- 2. Platysma and panniculus strong.
- 3. Digastric muscular and less extensive.
- 4. Palatal formula C11I5P+U-.
- 5. Absent.
- 6. Epiglottis notched.
- 7. No special gastric gland.
- 8. No precardial lymphatic gland.
- 9. Parotid glands small.
- 10. Sublingual glands small.
- 11. Cheek-ponches minute.
- 12. Two thoracic thymic lobes.
- 13. Spleen triangular.
- 14. Thyroid gland in posterior part of neck.
- 15. Well-marked cæcal mesentery.
- 16. Lower pole of right kidney level with hilum of left one.
- 17. Mammæ 8.
- 18. Large marsupium in adult.
- 19. Arterial canal of seventh cervical vertebra incomplete.

Cænolestes obscurus.

1. Absent.

- 2. Weak.
- 3. Digastric has aponeurotic attachment between symphysis menti and mandibular angle.
- 4. Formula $C_9I_5P + U .$
- 5. Labial labrets present.
- 6. Entire.
- 7. Present.
- 8. Present.
- 9. Large.
- 10. Large.
- 11. Large.
- 12. Four thoracic thymic lobes.
- 13. Spleen with lateral piece.
- 14. In anterior part.
- 15. Absent.
- 16. Kidneys at same level.

17. Mammæ 4.

- Marsupium absent in adult and rudimentary in the young.
- 19. Complete.

In my paper on the Koala and Vulpine Phalanger I tabulated the differences between them, and stated that the Phalanger has characters possessed in common by many Marsupials. The following list enumerates the points in which all forms differ from *Phascolarctos cinereus* :—

- 1. Hyoglossus muscle present.
- 2. Vena transverse horizontal.
- 3. Anterior palatal ridges convex forwards.
- 4. Tongue close to epiglottis.
- 5. Pylorus does not project into duodenum.
- 6. Tonsils in fauces.
- 7. Pharynx has no dorsal ridges.
- 8. Innominate artery present.
- 9. Postcava covers abdominal aorta.
- 10. Gall-bladder does not extend as far as the middle of the duodenum.
- 11. Pancreas dendritic.
- 12. Patella present.
- 13. Right lung has an azygos lobe.

I have nothing new to add to the well-known external and skeletal characters of the Marsupialia.

Summary and Conclusions.

1. The mylo-hyoid and sterno-hyoid muscles are attached to the hyoid bone, and the hyoglossus muscles are present in all Marsupials except *Phascolarctos cinereus*.

2. The sterno-facialis muscle may arise from the platysma by splitting.

3. The characters of the mouth and epiglottis are very variable in the Marsupialia, and I would urge that they be added to those at present in use for purposes of classification.

4. The right auricular appendix is not always bifid, as stated by Owen, and sometimes the division has no relation to the ascending aorta.

5. When a special gastric gland is present, the abdominal branches of the vagi are very numerous.

6. The Polyprotodonts have small parotids and large submaxillaries, but the reverse is the case in Diprotodonts. The largest glands are present in *Dendrolagus*.

7. The thyroid is thmus and anterior jugular veins are only found in *Trichosurus vulpecula*.

8. The postcaval vein covers the aorta in all Marsupials except *Phascolarctos cinereus* and *Petaurus taquanoides*.

9. The vagus and sympathetic nerves are fused in the neck in all Polyprotodonts and some Diprotodonts, but they are separate in a few Diprotodonts. From the examination of these nerves in all classes of vertebrates I have come to the conclusion that the former is the more primitive type. 10. The Polyprotodonts have more characters common to all genera than the Diprotodonts. And they retain primitive characters in their tongues, intestinal tracts, thymus glands, and nervous systems.

BIBLIOGRAPHY.

- BEDDARD, F. E.—"The Visceral Anatomy and Brain of Dendrolagus bennetti." Proc. Zool. Soc. Lond. 1895, pp. 131-137.
- CARLSSON, A.—" Über Dendrolagus dorianus." Zool. Jahrb. Jena, Systematik, xxxvi. pp. 547-617. 1913-14.
- 3. CUNNINGHAM, D. J.—'Challenger' Reports. Zool., V., pt. xvi. pp. 1–192. 1882.
- GARROD, A. H.—"On the Kangaroo called Halmaturus luctuosus by d'Albertis, and its Affinities." Proc. Zool. Soc. Lond. 1875, pp. 48-59.
- 5. MACKENZIE, COLIN.—Journal of Anatomy and Physiology, 1916, pp. 1–18.
- MITCHELL, P. CHALMERS.—"On the Intestinal Tract of Mammals." Trans. Zool. Soc. Lond. xvii. pt. v. pp. 437– 535. 1905.
- MITCHELL, P. CHALMERS.—" Further Observations on the Intestinal Tract of Mammals." Proc. Zool. Soc. Lond. 1916, pp. 190–199.
- 8. OPPEL, A.-Lehrbuch der verg. mikr. Anat. vols. i.-iii.
- Osgood, W.—"A Monographic Study of the American Marsupial Caenolestes." Field Museum of Nat. Hist., Zool., Chicago, May 1921.
- 10. OWEN, R.—The Comparative Anatomy of Vertebrates, vol. iii.
- 11. OWEN, R.—Art. "Marsupialia" in Todd's 'Cyclopædia of Anatomy and Physiology,' vol. iii.
- OWEN, R.—"Notes on the Anatomy of the Tree-Kangaroo (*Dendrolagus inustus* Gould)." Proc. Zool. Soc. Lond. 1852, pp. 103-108.
- 13. PARSONS, F. G.--" On the Anatomy of *Petrogale xanthopus*, etc." Proc. Zool. Soc. Lond. 1896, pp. 683-714.
- 14. POULTON, E. B.—" On the Tongues of the Marsupialia." Proc. Zool. Soc. Lond. 1883, pp. 599–628.
- SONNTAG, C. F.—"The Comparative Anatomy of the Koala and Vulpine Phalanger." Proc. Zool. Soc. Lond. 1921, pp. 547-577.
- 16. Swan, J. The Comparative Anatomy of the Nervous System of Vertebrates. 1864.
- 17. SYMINGTON, J.—"The Thymus Gland in the Marsupialia." Jour. Anat. Phys. xxxii. pp. 278-291. 1898.
- 18. SWALE, VINCENT.—Internal Secretion and the Ductless Glands. London, 1912, pp. 353-366.

- WINDLE, B., & PARSONS, F.—" On the Anatomy of Macropus rufus." Jour. Anat. Phys. xxxii., N. S. xii. pp. 119-134. 1898.
- 20. FLOWER, W. H.—"On the Organs of Digestion in Mammalia." Medical Times and Gazette, 1872, pp. 645-647.

21. RETTERER.-C. R. Soc. Biol. vol. 78, p. 535. 1915.

The papers by Carlsson, Osgood, and myself contain extensive bibliographies. Owen's article on the Marsupialia in Todd's 'Cyclopædia of Anatomy and Physiology' enumerates the older papers. The external characters of the Diprotodonts have been described by Pocock, P. Z. S. 1921, pp. 591–608.